NEW LOCATIONS AND INTERPRETATION OF VERNAL POOLS IN SOUTHERN CALIFORNIA

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ABSTRACT

An undocumented series of disturbed and remnant vernal pools was discovered during the abnormally wet 1992-1993 rainfall season in coastal southern California at San Clemente State Beach in southwestern Orange County, and from two sites at San Onofre State Beach in northwestern San Diego County. An additional series of remnant terrace vernal pools was found between Rancho Laguna and the City of San Clemente also in coastal Orange County. San Diego pools associated with either claypan or duripan soils have different suites of plant species despite their close proximity. The coastal Orange County pools, herein proposed as possible liquefaction-origin pools, also support a distinctive flora.

Aerial photographs of the region made prior to extensive urbanization show widespread fields of mima mounds (which coincide with present pool localities), likely indicating extensive historical vernal pool habitat. In coastal Orange County, remnant mima mound-type topography is present only at San Clemente State Beach and at Moulton Meadows in Laguna Beach; fragmented mounds occur in the Dana Hills and the City of San Clemente. We suggest that the origin of some mima mounds in coastal southern California may be attributed to Holocene seismic activity and liquefaction-related events. A biogenic maintenance hypothesis is proposed for the mima mounds: foraging activities by fossorial (burrowing) rodents in liquefaction terrain may play an important role in deterring long-term erosion of mounds and filling in of intermound pools. New word models are presented to explain how these relationships might have evolved including: "earthquake successional sequences" and "seismogenic tracker species." Earthquake successional sequences, including intermittent pools and mounds, provide habitat created by

ongoing seismic and liquefaction-related activities for invasion by seismogenic tracker organisms, which possibly include fairy shrimp, western spadefoot toad, pocket gophers, and other opportunistic species whose mode of life is in part associated with seismic-induced terrain.

We describe the previously unrecognized role of cryptogamic vegetation in regulating microscale gradients such as moisture status, nutrient availability, soil temperature, microbial processes, and safe-site seed selection which directly affect the biology of vernal pools. The cyanobacterium, *Microcoleus vaginatus*, is identified as a potential keystone organism occupying vernal pools and astatic alkaline sinks in southern and central California. A preliminary catalog of the cryptogamic and phanerogamic flora of vernal pools and adjacent upland terrain is presented. A number of rare or regionally uncommon vascular plants were collected during this study including *Atriplex pacifica*, *Dudleya blochmaniae*, and *Myosurus minimus*. New records documented for Orange County include the native *Trifolium variegatum* and the exotics *Atriplex lindleyi* and *Hainardia cylindrica*, *Glinus lotoides*, introduced from Europe, is new for San Diego County.

KEY WORDS: Vernal pools, California, Orange County liquefaction-origin pools, San Diego County duripan/claypan pools, fossorial rodents, mima mounds, Holocene earthquakes, seismogenic tracker species, cryptogamic crusts, *Microcoleus vaginatus*, keystone species, fairy shrimp

INTRODUCTION

California's vernal pools are small to medium sized temporary ponds which form above hardpan, claypan, or volcanic mudflow soils during the winter rain season but drain completely by late spring (Bauder 1986); vernal pools are often defined and identified by their endemic or regionally restricted flora (Thorne 1984). They range in size from a few square meters to several hectares and are always shallow, most by 10 to 60 centimeters (Zedler 1987). Pools larger than 20 hectares are referred to as vernal lakes (Holland 1976). Vernal pools are also surface water depression wetlands according to Novitzki (1979). Perched above an impermeable soil layer and separated from groundwater or stream channel inflow, a vernal pool fills only by slowly collecting precipitation, although the wet-life of vernal pools may be extended by subsurface flows (Hanes, *et al.* 1990). Although evaporation exceeds precipitation in most coastal southern California wetlands (Stevenson & Emery 1958), vernal pools also share characteristics of ombrotrophic (rainy) environments since precipitation-dominated wetlands receive nutrient inputs primarily from wet and dry atmospheric deposition (Doss 1995). Despite the recognized importance of hydrogeologic regimes in driving nutrient dynamics in wetlands (Carter 1986; Labaugh 1986), the relationship between hydrologic processes and nutrient cycling in vernal pools has not been addressed.

Zedler (1990) has likened the winter vernal pool habitat to a cool-temperate pond, and in late spring to autumn, a desert. Nestled within a subtle upland depression, the pool erratically fills and empties, often repeatedly throughout the season due to uncertain rainfall before completely drying by evapo-transpiration. The dry vernal

pool pan, also described as a dry marsh bed (Kopecko & Lathrop 1975), may persist for years without filling completely, especially during severe drought. Winter ponding deters most aggressive upland plants from invading a vernal pool; and in shallow pools, the relatively short-lived inundation period also slows development of the permanent anaerobic conditions necessary for establishment of many marshland species.   The recurrent inflow of rainwater produces an ephemeral amphibious environment with micro-niches for vascular plant and cryptogamic species including an easily overlooked, shallow undulating pool margin that simulates a tidal mud flat. Alternating winter inundation and summer drought has selected a unique assemblage of amphibious plants and animals including specialized endemics as well as a group of aquatic generalists capable of tolerating a double-stress regime.   Zedler (1990) developed the "recurrent gap" hypothesis based upon the reliable recurrence of microhabitats due to uncertain rainfall to explain traits in annual seed plants; accordingly, we emphasize the importance of the "recurrent flux" of inundating rainfall in the creation of niches for cryptogams in vernal pool terrain.

The floristic composition of a vernal pool may be perpetuated for decades because southern California's arid climate does not support peat formation, a process that speeds up plant community succession; the amphibious character of this habitat and its specialized biota are closely dependent on California's Mediterranean-type climate which is characterized by mild, moderately wet winters and rain-free summers. Zedler (1987) describes four stages of pool development: 1) a wetting phase; 2) an aquatic phase; 3) a drying phase; and 4) a drought or dormant phase. Vernal pool plants and animals often depend upon one or more of these specific phases (Zedler 1987; Holland & Jain 1984).   Although Zedler (1987) indicates that climate is key for the establishment of true vernal pool habitat, edaphic factors may be more important with respect to the vegetation than climate (Holland & Dains 1990).

Vernal pools are not unique to California (Thorne 1984), but their plant communities of course are (Holland & Jain 1977). Intermittent pools and pool-forming processes that most closely simulate and support biota characteristic of California's vernal pools, occur primarily in other Mediterranean climate regions (*i.e.*, South Africa, southwestern Australia, the Mediterranean Basin, and Chile). Phytogeographic phenomena, including amphitropical disjunctions of the same or similar phanerogamic species between the pools of temperate North and South America, also link the vernal pool biota of the Mediterranean climate regions. Long-distance dispersal by migrating birds is probably involved (Raven 1963). Members of California's vernal pool flora which have disjunct austral counterparts include species of *Marsilea*, *Crassula*, *Isoetes*, *Myosurus*, and *Eryngium* (Zedler 1987).   New information on the phytogeography of cryptogamic vegetation suggests that species shared between southern California and other Mediterranean climates may be relicts of an ancient Madro-Tethyan flora rather than products of long-distance dispersal, which is less likely for many lichens and bryophytes. The cryptogamic flora of South Africa and California, unlike the vascular flora, does share identical and vicariant taxa, *i.e.*, *Buellia halonia* (Ach.) Tuck., *Punctelia punctilla* (Hale) Krog, and *Trichoramalina crinitum* (Tuck.) Rundel & Bowler/*T. melanothrix* (Laur.) Rundel & Bowler (Bowler & Rundel 1974; Riefner 1989; Weber 1993).   The recent discovery of *Ramalina canariensis* Steiner in California (Riefner & Bowler 1994), previously documented from all the Mediterranean climate regions except California, points to our lack of understanding of dispersal mechanisms and relict endemism on the continental level.

Additional study may yet link the cryptogamic vegetation of California's vernal pools with that of other Mediterranean climates.

Vernal pools and much of their biota are considered to be the most specialized and endangered type of wetland in California (Bauder 1986; Cheatham 1976; Cochrane 1985; Ferren & Pritchett 1988; Ferren & Fiedler 1993; Holland & Griggs 1976; Thorne 1984; Zedler 1987). The rigors of the habitat have provided fertile ground for rapid evolutionary radiation in the vascular flora (Stone 1990). Noteworthy are several characteristic genera of annual plants including *Downingia*, *Eryngium*, *Lasthenia*, *Limnanthes*, *Navarretia*, *Orcuttia*, *Plagiobothrys*, and *Pogogyne*. Many taxa often belong to a suite of narrowly restricted species which occupy a particular pool type characterized by specific soil properties, inundation regimes, and/or elevation (Bauder 1993). The likelihood that a particular suite of species is present in any one pool group is determined by a highly localized set of gradients that may not be widely encountered. Bauder (1993) has discussed differences in microscale gradients of soil and elevation affecting vernal pool plants in San Diego County, including highly localized species such as *Pogogyne abramsii* J.T. Howell and *Downingia concolor* E. Greene subsp. *brevior* McVaugh. Similar evidence documenting the microscale conditions of soils and inundation regimes for specific suites of species in Merced and Placer counties was presented by Holland & Jain (1990). Selective pressures exerted by multiple local and microscale parameters including soils, inundation regimes, temperature, and factors such as fungal associates which may affect germination have contributed to the complexity of vernal pool ecology and evolution.

Holland & Jain (1990) believe that floras of vernal pools differ according to soil type, while Bauder (1987) and Zedler (1987) state that local pool composition and structure in southern California are best explained by frequency and duration of ponding. We believe a more intricate web of functionally linked physical-hydrogeologic and biological processes including local hydrologic cycles and climate patterns, landform age and origin of mound-depression microrelief, nutrient cycling, microbiota and cryptogamic vegetation, abiotic and biotic factors which maintain mound-depression terrain, site history, and disturbance all interact to affect the diversity and abundance of plants and other organisms in southern California's vernal pool terrain.

Vernal pools occur within an upland vegetation matrix of grassland, chaparral, coastal sage scrub, and/or oak woodland habitat. Because of their isolation, vernal pools have frequently been referred to as terrestrial or ecological islands (Holland & Jain 1988; Zedler 1987; Schoenherr 1992; Stone 1990). The quasi-endemic nature of vernal pool "island plants" is due in part to lack of seed dispersal mechanisms which favors keeping the seed supply on-site. Zedler (1990) compiled data indicating that nearly three-quarters of the vernal pool species in San Diego County have no obvious means of dispersal. Clusters of "island" pools have been referred to as archipelagoes, suggesting that principals of island biogeography might be used to unravel complex phytosociological patterns correlated with pool numbers and size (Holland & Jain 1981, 1988).

In this paper, we refer to local patches of remnant pool habitat as islands within an upland vegetation matrix, and to chains of such patches as archipelagoes (Burkey 1995). Herein, we report new localities of San Diego claypan and duripan vernal pool

habitat and a new archipelago comprised of the previously uncharacterized Orange County vernal pools. The San Diego and Orange county pools each support different suites of plant species. The ready accessibility of these pools with their distinctive floras offers a rare opportunity to study the complex, and still incompletely known, biotic interactions within vernal pool communities.

DISTRIBUTION OF CALIFORNIA VERNAL POOLS

In western North America, vernal pools have been reported from southern Oregon southward into Baja California, México (Holland & Griggs 1976; Kagan 1986; Moran 1984). The vernal pools of California primarily occur in two clusters: 1) the coastal terraces and areas of gentle topography of the lower coastal mountains from Sonoma to San Diego County; and 2) from Shasta to Kern county in the Central Valley (Zedler 1987; Holland & Jain 1977; Ferren & Pritchett 1988). Vernal pool vegetation is best developed in the eastern Central Valley on ancient terrace soils bordering the foothills of the Sierra Nevada, where concentric rings of wildflower displays· unmistakably reveal the presence of vernal pool terrain (Holland & Jain 1988). Holland (1978a; 1978b) states that vernal pools were apparently a common feature in most of the Central Valley in presettlement times, estimating that nearly one-third of the valley historically supported them. However, vernal pools in other regions of the state have not been studied as thoroughly, so we cannot adequately assess their historic range and estimate habitat loss.

In southern California, Ferren & Fiedler (1993) estimate that as much as 90% of the vernal pools have been destroyed in the past century. In San Diego County, vernal pools were once common on coastal terraces and inland valleys (Purer 1939). Many have been destroyed by development. Current estimates indicate over 93% of the county's vernal pool habitat has been extirpated, and many of the remaining pools are highly disturbed (Bauder 1986). The situation is similar in Orange County. Aerial photographs of northwestern San Diego and southwestern Orange counties taken prior to extensive urbanization (1932 Whittier Collection; 1941 USGS; 1953 USDA; 1964 California Coastal Commission) show widespread fields of mima mounds, indicating extensive historical vernal pool habitat.

Vernal pools are well known in San Diego and Riverside counties, but not in Orange County, where the pools have remained undocumented. This overlooked habitat has been omitted in important studies of critical plant communities, such as Horn, et al. (1993) and Sawyer & Keeler-Wolf (1995). Evans & Bohn (1987) identified mima mound topography in southern Orange County, and Marsh (1992) described remnant or extirpated pools from the Laguna Beach area and Dana Point. Marsh (1992), however, did not cite any of the vernal pool obligate species discussed by Zedler (1987) and therefore, could not authenticate the presence of true vernal pool habitat. Marsh (1992) believes that vernal pools were once common in southern Orange County.

Remnant Orange County terrace vernal pools were identified during this study utilizing aerial photography provided by G. Kuhn (1993, pers. collection), soil survey, and herbarium specimen data. Several pools were documented between

Rancho Laguna and the City of San Clemente only during the unusually wet 1992-1993 rainfall season (Orange County Environmental Management Agency 1996). Aerial photographs taken prior to urbanization in south-central Orange County (City of Irvine, University of California Campus) depict vernal pools (1971, W. Bretz-NRS Collection). Other vernal pools recently recorded from Orange County occur at Whiting Ranch and O'Neil Park (Jones & Stokes 1993), and in Fairview Park, Costa Mesa, (Bowler, *et al.* 1995). A series of small pools also occur near the Badlands Park in Laguna Beach (P. Bowler, pers. comm.). The remaining vestige of pools in Orange County are possibly remnants of a once broader complex of coastal terrace habitats that has been nearly extirpated because of urbanization and agriculture. Soil surveys show that vernal pools in coastal southern Orange County are developed primarily over the very slowly permeable, moderately alkaline Myford sandy loam or the moderately slowly permeable Botella clay loam (Soil Conservation Service 1978). A map and detailed study of the flora of these pools is in preparation.

THE ORIGIN OF MIMA MOUNDS

Mima mounds are the elevated, often circular areas between vernal pools that are composed of unconsolidated fine soils; the term mima mounds originates from their type locality, Mima Prairie, near Olympia, Washington (Dalquest & Scheffer 1942). Mima mounds and vernal pools are inexorably intertwined; there are no mounds without intervening depressions. In California, the intermound depressions are also known as hogwallows (Arkley & Brown 1954; Brandegee 1890; Cox 1984a). Although climate is key for the formation of vernal pools, topography is also important, since pools mostly form in closed depressions (Zedler 1987). In North America, mima mounds are recorded only west of the Mississippi River ranging from southern Canada to northern México (Cox & Scheffer 1991).

Studies of mima mound formation have produced a number of controversial theories about the origins of the mounds. Washburn (1988) provided a comprehensive review, and Berg (1990) grouped theories into four categories: 1) depositional; 2) erosional; 3) periglacial; and 4) biological. Cox (1984b), Zedler (1987), and Holland & Jain (1988) described mound-building processes pertinent to California including origin by: 1) wind deposition near the base of shrubs; 2) groundwater pressure; 3) the activities of fossorial rodents; 4) fracture patterns in the underlying hardpan; 5) expansion and contraction of clay minerals upon wetting and drying; and 6) subsurface mass movements such as soil-piping. Zedler (1987) proposed that differential weathering and settling is primarily responsible for mounded topography in California and presented a model for mound origin by weathering. Each one of the foregoing theories can be locally confirmed by data from particular localities, but none hold true for all situations (Holland & Jain 1988). In recent years, however, only the fossorial rodent hypothesis has received broad acceptance (Dalquest & Scheffer 1942; Arkley & Brown 1954; Barry 1981; Cox 1990).

According to the fossorial rodent hypothesis (Cox 1984; Cox & Scheffer 1991), moundfields originate in shallow soils where pocket gophers build nest sites to escape predation and weather. The nest sites become the center of fixed territories. Subsequently, gophers mine and translocate soil in slow centripetal fashion toward

nests. This tunneling translocates soil, which in time, builds mounds until the centripetal soil-mining activities are balanced by unknown factors (Cox & Scheffer 1991). Cox (1984a,b) has provided evidence that mound formation by foraging rodents is plausible; estimating a typical mound could be formed in approximately 108 years. Extensive behavioral documentation of gophers by numerous researchers has apparently corroborated the pocket gopher theory (Gregory, *et al*. 1987; Hansen 1962; Howard & Childs 1959). Scheffer (1958) and Cox & Scheffer (1991) believe that mima mound terrain occurs only where rodents are, or have been, working the soil.

Although there is an extensive literature discussing the biogenic origin of mounded landscapes, geologists have remained skeptical. Berg (1989) proposed that mounded landscapes are formed when strong seismic activity occurs in areas where a shallow mantle of loess or other fine unconsolidated material overlies a relatively rigid, planar substratum. The substratum could be hardpan, bedded gravel, or bedrock. Berg (1990) then presented data showing that the circular shape and the uniform pattern of mounds can be explained by Richter's (1958) theory of seismic wave motion. According to Berg (1990), the distribution of mima mounds in the United States is directly correlated with regions of moderate to high seismicity. The seismic hypothesis could account for the presence of mima mound-type topography in a wide variety of global geomorphic and climatic provinces and could also explain mound uniformity and soil profiles of mima mound landscapes that cannot be easily demonstrated by the pocket gopher or other theories.

Recently, Kuhn, *et al*. (1995a) identified liquefaction-related features including fissure fills and lateral spreads in mima mound terrain near Carlsbad, San Diego County, in coastal southern California. Paleo-liquefaction, as postulated by these authors, is conspicuous at the Carlsbad site as widespread and abundant injection dikes composed of fine grained white sand, inferred to be ancient beach sand, thrust through the plastic clay-rich surficial deposits; the injection dikes are "sand blow deposits," previously described by Fuller (1912) and Sieh (1978). Existing sand blow deposits (mima mounds) are correlated with the extent of an ancient intertidal lagoon. Kuhn, *et al*. (1995b) hypothesize that during or since the Holocene, mima mound formation due to liquefaction only occurred rarely, when a strong earthquake coincided with unusually high rainfall and perched water conditions far above modern groundwater levels. Although the age of the liquefaction event(s) remains to be determined precisely, the size of the sand blow deposits, the area affected, and the uplift of ancient intertidal deposits imply that coastal uplift and mima mound formation occurred as a result of large, infrequent pre-historic earthquake(s) of magnitude seven or greater. Legg, *et al*. (1994) and Kuhn, *et al*. (1995a) suggest that the source of seismic activity may well be the Newport-Inglewood/Rose Canyon fault located four to six kilometers off the southern California coast. Later studies by Kuhn, *et al*. (1995b) have identified paleo-liquefaction features which extend upward into a series of regressive continental deposits that overlie flights of marine terrace platforms ranging in elevation from 10 to 60 meters. Cross-cutting stratigraphy and relative weathering show at least three epochs of paleo-liquefaction in this region that have displaced very old Indian middens and other archaeological sites (Kuhn, *et al*. 1995b). Thus, major Quaternary deformation of the southern California coast induced during large strike-slip earthquakes are recorded by liquefaction features which could be important in the formation of vernal pools located on higher terraces in Orange and San Diego counties.

Norwick (1991) described the relationship between vernal pool formation and geomorphic processes. He identified ongoing tectonic activity, including development of surface folds and shutter ridges (when a fault moves rock masses horizontally across a valley) with the formation of sag ponds, vernal pools, and swale topography. Norwick's "sand volcanos" and liquefaction craters described from the San Andreas Fault zone were formed during the earthquake of 1906, and apparently predate other intermittent pools of the region.   Sieh (1978) also identified liquefaction-related features, including sand blow deposits, as by-products of slip along the San Andreas fault.

Previously, Fuller (1912) studied the succession of shocks collectively designated as the New Madrid earthquake, which occurred between 1811 and 1812, in the central Mississippi Valley in an area encompassing portions of Missouri, Arkansas, Kentucky, and Tennessee.   No other feature of the New Madrid region is so conspicuous or widely encountered as the "sunk lands" which resulted from local settling or warping of alluvial deposits (Fuller 1912). Sunk lands are characterized by major alterations to or creation of wetland habitats in clayey alluvial deposits that were still evident 100 years following the shocks.   These include sand sloughs, river swamps, sinks, lakes, and ponds. Fuller also describes in great detail sand blows and fissures, which are presently interpreted as relict features of liquefaction events (Obermier 1989). Fuller cites numerous historical accounts of fields composed of sandy mounds, including (pg. 81): 1) "In several places the [sand] blows so obstruct the drainage as to cause the water to collect in shallow pools throughout the wet season."; 2) "The [sand] blows were so thick as to touch, giving rise to many irregular depressions, in some of which considerable pools of water accumulate."; and (pg. 83) 3) "The country here was formerly perfectly level and covered with prairies of various sizes dispersed through the woods. Now it is covered with slashes (ponds) and sand hills or montecules, which are found principally where the earth was formerly the lowest. . . ." The sand blow regions coincide with Berg's (1990) regions of past moderate to high seismicity. Fuller also documents sand craterlets formed near San Francisco in the earthquake of 1906.

The seismogenic origin of mounded landscapes proposed by Berg (1990) and Kuhn, *et al.* (1995b) works also for coastal southern California. It is plausible that the origin of mima mound terrain is, in part, a product of paleo-liquefaction induced by large pre-historic earthquakes, possibly occurring since the Holocene. The impact of shaking on mound-pool terrain could produce settling of fine mound sediments even when earthquakes are not powerful or when they do not coincide with perched water conditions. If mima mounds in coastal southern California were originally formed by successive episodes of liquefaction (presumably southern California has been subjected to large seismic events which induced mound-pool formation long before the Holocene), what ongoing factors operate to maintain the circular profile and height of mounds and deter siltation of fine sediments and sand into intermittent pools? We suggest a biogenic maintenance of liquefaction-mounded landscapes by the activities of fossorial rodents.

As discussed above, evidence has been accumulating for decades indicating that pocket gopher activity is associated with mima mound terrain (Dalquest & Scheffer 1942; Arkley & Brown 1954; Barry 1981; Cox 1990). Soil mining and translocation within "mima mounds" by pocket gophers could replace fine sediments easily lost to erosion, accounting for the long-term maintenance of the mounds' circular form and

height. Tunneling and soil translocation may also impede the otherwise inevitable siltation of intermound basins. Cox (1984b) believes the activities of fossorial rodents create intermound basins while Kuhn, *et al.* (1995a) state that some vernal pools originate over liquefaction-related laterally spreading clays.

Kuhn (unpublished data) has observed vacant rodent burrows in liquefaction terrain in southern California. Abandoned or declining gopher populations in mima mound terrain could produce a mosaic of swales and cloudy silt-pools that provide favorable habitat for other organisms including fairy shrimp, but not for vernal pool obligate plants. Some species of fairy shrimp are not randomly distributed in natural temporary ponds but may favor pools with turbid water to avoid Notonectid (*i.e.*, backswimmer) predation (Woodward & Kiesecker 1994). Shallow silt-pools lack inundation regimes necessary to sustain year to year vernal pool obligate plants except during abnormally high rainfall years. However, cloudy later succession "seres" of intermittent pools could be important in the distribution of vernal pool plants and other species which lack long-distance dispersal mechanisms by providing local habitat patches in the chain of biological archipelagoes. Seed and other propagules could be dispersed between vernal pool "islands" by birds (Baker, *et al.* 1992). Study of liquefaction terrain could afford insight into abiotic and biotic processes affecting possibly coevolutionary biological interactions in earthquake landscapes.

The widely accepted hypothesis that the origin of mounded topography and associated intermittent pools in California is the result of only a single or simplified process should be reevaluated. Vitek (1978) also concluded that mounded topography may result from various processes, and Fuller (1912) described the differences in the genesis of sand blow mounds and prairie mounds. In California with its complex geologic history, mound-depression landscapes can be attributed to numerous and often complementary processes, so that interacting biotic and abiotic processes need to be quantified at each site. In coastal southern California on high geomorphic surfaces (pre-Holocene), mound topography could have a complex origin; mounds may have formed when the surfaces were at low elevations, particularly in sandy sediments conducive to liquefaction, but after uplift, the mounds would have been modified by fossorial rodent activity (R. Shlemon, pers. comm.). Mima mounds and pools developed on specific geologic formations or soil series with different inundation regimes, water-retention capacities, stability and sediment shedding characteristics would be expected to support distinctive floras and faunas.

Liquefaction-origin pools developed in sandy substrates are prone to wetted-clay slip and external drainage; human disturbance could easily reduce the frequency and duration of ponding in vernal pools. As a result, liquefaction-terrain vernal pools may not be recognized readily and their accompanying biota could be overlooked; clearly, this has been the case in Orange County. Mima mounds composed of white or tan fine sands occurring in proximity to major fault zones or in soils without an argrillic horizon, especially those on coastal terraces or inland dunes, may be suspected of liquefaction origin (G. Kuhn, pers. comm). Aerial photographs depicting white, circular spots may indicate remnant mima mounds (*i.e.*, sand blow features) that have been mechanically bladed or disced (Kuhn, *et al.* 1995a). Vernal pools on uplifted marine terraces in the San Diego area previously discussed by Purer (1939) should also be inspected for liquefaction features.

FLORISTICS AND ECOLOGY OF CRYPTOGAMIC VEGETATION IN VERNAL POOL TERRAIN

One of the most widely discussed topics of California natural history is the distinct, concentric assortment of vascular plant species which describe subtle topographic gradients in vernal pools. In southern California the floras of vernal pools differ (Bauder 1987), but whatever species are present selectively inhabit micro-niches or broad radial zones related to inundation regimes, and perhaps, nutrient availability. Kopecko & Lathrop (1975) describe five habitat zones for vascular plants in vernal pools on the Santa Rosa Plateau in western Riverside County, but cryptogamic species also display this kind of zonation.

Cryptogams in vernal pools have scarcely been studied in California, and their contribution to the ecology of this ecosystem has been severely neglected and warrants immediate attention.   A preliminary survey of southern California vernal pools suggests a cryptogamic community dominated by cyanobacteria, bryophytes, and cyanophilous lichens (lichens that have blue-green algae photobionts) occupy zones similar to those of the specialized vascular plants.   Kopecko & Lathrop's (1975) "muddy margin zone" and the "vernally moist zone" are occupied and often temporarily dominated (extending from the pool basin to mesic margin) by such organisms including species of *Nostoc* (cyanobacterium), *Scleropodium* (moss), *Microcoleus* (cyanobacterium), *Fossombria* (liverwort), *Collema* (cyanolichen), *Riccia* (liverwort), *Funaria, Bryum,* and *Ceratodon* (mosses).   *Nostoc, Leptodictyum* (moss), *Microcoleus,* (?) *Fissidens* (moss), and *Scleropodium* often thrive in the "vernally standing water zone" of vernal pools, and species of *Bryum, Funaria,* and *Microcoleus* are common invaders of the "drying marsh bed." A narrow, ephemeral band of bryophytes dominated by liverworts which occurs between the "muddy margin and vernally moist zones" indicates seasonal or year to year fluctuations in precipitation.   Lichens most frequently become a prominent feature in the "dry grassland/scrub zone" of undisturbed vernal pool landscapes and may include species of *Acarospora, Catapyrenium, Collema, Cladonia, Psora, Toninia,* and *Trapeliopsis.* The lichens are successionally dominant to mosses and even certain grass and forb species in specialized habitats (Coker 1966; During & Van Tooren 1990; Watt 1937), such as southern California coastal cliffs, dunes, volcanic tablelands, and littoral communities, but are not dominant in inundated areas of vernal pool landscapes. Later successional bryophyte species and cyanophytes such as *Microcoleus vaginatus* (Vauch.) Gom. are also important in native grasslands and scrub in southern California.   The absence of cryptogamic flora from suitable habitats in and around vernal pools indicates disturbance and/or alteration of hydrologic cycles by human activities including habitat fragmentation, grazing and discing, alteration of the fire ecology, and air pollution (Bowler & Riefner 1990). It should be noted that pristine floras such as the Morro Bay region in San Luis Obispo County support nearly 375 lichen taxa (Riefner, in prep.); the depauperate list of cryptogams presented in this paper is typical of urban environs in coastal southern California.

Cryptogamic soil crusts (also called biological, cryptobiotic, organogenic, and microphytic crusts) are formed by complex communities of several groups of microphytes including mosses, lichens, liverworts, fungi (including mycorrhizal fungi), green algae, cyanobacteria (blue-green algae), and bacteria. Soil crusts are

common in arid and semi-arid landscapes, and when well-developed, cover the ground with an almost continuous sheet of photosynthetic machinery equivalent to a layer of phanerogamous leaves (Lange, *et al.* 1994). Although usually not thicker than a few millimeters, soil crusts play a decisive role in the functional ecology of arid ecosystems, including cycling of nutrients (especially nitrogen), soil aggregation and stabilization, carbon gain in large areas (Eldridge & Greene 1994; Lange, *et al.* 1992; Beymer & Klopatek 1991), and soil fertility and microbial food webs (Harper & Marble 1988; Johansen 1993; Belnap & Gardner 1993; Belnap 1995). More importantly, cryptogamic crusts deter surface evaporation by sealing the soil surface, and improve overall moisture storage (Lange, *et al.* 1992). During rains, these crusts produce a high yield of runoff percolation which does not occur if crusts are broken or absent (Yair 1990; Lange, *et al.* 1992). Claims of reduced erosion and improved water relations due to cryptogamic vegetation have been widely reported in the literature, but until recently, the evidence has been largely circumstantial. Several authors, however, have recently described and experimentally reproduced the mechanisms by which cryptogams protect the soil and regulate water flow (Chartes & Mucher 1989; Eldridge & Greene 1994; Tchoupopnou 1989; Kinnell, *et al.* 1990; Yair 1990). Thus, the presence or absence of cryptogamic crusts in arid regions can influence the hydrologic cycles of total landscapes including soil erosion (Cameron & Blank 1966; St. Clair & Johansen 1993; West 1990). Despite their importance and widespread distribution, our present knowledge of the species composition and mode of life of cryptogamic crusts is extremely limited in California where research has largely focused on the study of higher plants.

In undisturbed vernal pool landscapes cryptogamic crusts are often a prominent feature that are easily destroyed by grading, discing, grazing, alteration of the fire ecology, and trampling. In a dry climate, human alteration of gently mounded topography characteristic of vernal pool terrain can easily disrupt the delicate balance of specialized hydrophytes inhabiting the narrow radial zones of shallow pools. Additional loss of rain inception and runoff generated percolation historically produced by cryptogamic crusts may dramatically influence the hydrologic status of disturbed vernal pools in southern California, where the average rainfall is markedly less than in the northern part of the state. Increased erosion and decreased aggregate soil stability associated with degradation of cryptogamic communities of disturbed sites (Eldridge & Greene 1994; Kinnell, *et al.* 1990) could also negatively affect the biology of vernal pool terrain. The impact of severe erosion in vernal pool terrain is likely to be greater due to increased transport of organic nitrogen by eroded sediments where the erosional products are nutrient-rich silt and clays rather than sand (Burwell, *et al.* 1975; Pallis, *et al.* 1990; Kinnell, *et al.* 1990). Disturbance of soil surface crusts can also affect vascular plants due to disruption of food webs and alteration of the soil microbiota including mycorrhizal and rhizosheath associations (Allen 1991; Fitter 1977; Grime, *et al.* 1987; Hardie & Leyton 1981; Hartnett, *et al.* 1993), decreased water availability and nutrient uptake in vascular plants (Belnap 1995; Harper & Pendleton 1993; Rogers & Burns 1994), and decreased germination and seedling establishment (Lange, *et al.* 1994; Harper & Pendleton 1993; Rogers & Burns 1994; West 1990). The absence and/or reduction of cryptogamic crusts throughout much of southern California's remaining vernal pool landscapes raises many questions critical to the long-term management of this threatened, arid-land resource.

The microphyte-rich communities inhabiting southern California's vernal pool landscapes support several interesting, strongly interacting associations occupying the

muddy margin and vernally moist zones which could potentially affect the biology of other pool species. During an ongoing investigation of vernal pools in southern California, observations by the senior author of several undisturbed and disturbed pool complexes indicate the dominant constituent of these crusts, the cyanobacterium (blue-green alga) *Microcoleus vaginatus*, could influence or directly regulate several microscale gradients which affect seed plants competing for limited resources in narrow zonal boundaries. This paper presents several mechanisms by which cryptogamic crusts dominated by *M. vaginatus* regulate microscale gradients including water relations, nutrient availability, microbial processes and soil microbiota, soil temperature, safe-site seed selection, and seedling enhancement in vernal pools.

Microcoleus vaginatus is a filamentous, black, mat-forming species which secretes a mucilaginous polysaccharide material from a network of filaments which bind other microphytes and fine sediments into a well-developed crust (Belnap 1993a). *Microcoleus vaginatus* commonly comprises the major component of cryptobiotic crusts in many western states (Belnap 1993a). The success of this cyanophyte in occupying a wide habitat range is due to its resistance to temperature extremes, hypersalinity and alkalinity, desiccation, and to modest nutrient requirements (Carr & Whitton 1982). *Microcoleus* is ubiquitous, and the crust is often inconspicuous as a dark film in the "dry grassland zone" of Kopecko & Lathrop (1975). *Microcoleus*, however, develops a conspicuous mat or crust in vernally moist to inundated clay depressions in grasslands, alkaline sinks, and vernal pools if alternating cycles of wetting and exposure are present which favor rapid filament and sheath production. During the aquatic phase of vernal pools, *M. vaginatus* is often the locally dominant organism forming extensive mats over a broad zone extending from the outer pool edge to standing pool water. As ponded waters fluctuate, the *Microcoleus* colony simultaneously swells into a motile mat covering exposed mud to reach favored photic zones. During the drying phase of vernal pools as the perimeter retreats, *Microcoleus* does also, often coinciding with the germination of vascular plants. The desiccating mat forms a crust/shell over saturated pool soil, deterring evaporation and enhancing the life of an anaerobic zone which inhibits upland vascular plants from colonizing pool margins, and importantly, promotes growth of vernal pool obligates by providing fuel in the form of ammonia. After completely drying, "the dry marsh bed" of shallow pools is often richly covered by *Microcoleus*, and in late spring and summer the curling crusts are a conspicuous feature of many alkaline sinks and vernal pools. This feature could be useful for identifying seasonal wetlands and perched water conditions in southern and central California.

Two key ecophysiological characteristics of *Microcoleus vaginatus* could account for possible mechanisms that effect important microscale gradients.

(1) *Microcoleus vaginatus* produces a large, distinct, sticky extracellular sheath that surrounds groups of living filaments (Belnap 1992). Sheath material rapidly absorbs water, and when wetted, swells, then mechanically extrudes through or over the soil; as the substrate dries the filaments secrete additional mucilaginous material. Rewetting repeats this cycle. *Microcoleus vaginatus* frequently develops a mat or drying crust several millimeters thick due to the recurrent flux of vernal pool waters. *Microcoleus* is capable of growing up to five centimeters in 24 hours (Belnap, *et al.* 1993b) when wetted which enables it to reach favorable photic zones along fluctuating or subsiding pool waters. These adaptive mechanisms may maintain the mat in an

active state in exposed circumstances during alternating cycles of inundation and exposure.

(2) A second trait of *Microcoleus vaginatus* and other cyanophytes is the ability to fix atmospheric nitrogen throughout most of the year (Fuller, *et al.* 1960). Cyanophytes produce nitrogenase, an enzyme complex responsible for catalyzing the conversion of dinitrogen to ammonia. Nitrogen fixation is a stringent anaerobic process, and since *M. vaginatus* lacks heterocysts (thick-walled cells that exclude oxygen), an anaerobic microenvironment must be supplemented in other ways for nitrogenase activity to produce ammonia. Belnap, *et al.* (1993b) has postulated that *M. vaginatus* creates an oxygen-free zone by packing multiple filaments within thick extracellular sheaths or packing groups of sheaths together which has been demonstrated by the morphologically similar oceanic species *Microcoleus chthonoplastes* (Paerl 1985, 1990; Paerl, *et al.* 1991; Pearson, *et al.* 1981). Nitrogenase and N-fixation activity may be closely related to growth of new sheath material and/or new filaments produced only when this cyanophyte is wetted (Belnap, unpublished data). Asexual reproduction by mat expansion acts as a nitrogen source and sink which is mobilized by the presence of water.   .

Several other nitrogen-fixing lichen and cyanobacteria species are present in vernal pool habitats including *Nostoc* sp. (which does develop heterocysts not requiring constant anaerobic conditions) and the cyanolichen *Collema tenax* (which hosts *Nostoc* as its phycobiont). The cyanolichens apparently occur in numbers too small to contribute significant fixed nitrogen into this system, but species of *Nostoc* may, particularly in deeper static pools. *Nostoc*, previously discussed by Zedler (1987), is a colonial cyanophyte visible in vernal pools or more frequently along the edge of drying pools as small translucent balls. *Nostoc* is well documented for salinity tolerance, importance in nitrogen fixation, and use as a biofertilizer (Singh 1961; Singh, *et al.* 1996).

Microcoleus may serve an important function in the population structure of many vascular plants competing in zonal boundaries and microhabitats of vernal pools. The rapid growth and mat/crust-formation of *M. vaginatus* not only deters evaporation but maintains and enhances an anaerobic environment for itself and associated seed plants in microzones. These affects, in concert with specialized germination requirements, perpetuate native annuals and exclude exotics, and explain the resistance of vernal pools to upland plant invasion. Most importantly, ammonia enrichment produced by *Microcoleus* could alter competitive interactions and provide fuel for the explosive growth and reproduction of vernal pool annuals. Numerous studies have demonstrated that the nitrogen fixed by cyanobacteria is available to and is used by neighboring vascular plants (Fuller, *et al.* 1960; Maryland, *et al.* 1966; Maryland & McIntosh 1966; Stewart 1967). Also, nutrient uptake of seed plants associated with cyanobacterial crusts has been demonstrated to show higher concentrations of many essential macronutrients (Harper & Pendleton 1993; Belnap 1995). In some ecosystems, these crusts have been demonstrated to be the dominant source of limiting elements for seed plant communities (Evans & Ehlringer 1993). In other studies, Lange (1974) demonstrated that compounds in the gelatinous cyanobacterial sheath material were able to chelate elements essential for growth. Since both clay particles and organic material are negatively charged, the sheath material electrostatically absorbs positively charged essential nutrient ions and holds them in a form available to higher plants (Lange 1976). The sheath material of *Microcoleus* may also enhance the

availability of iron to vascular plants (Belnap & Harper 1994). Chelation of iron may be especially important in alkaline soils (such as the vernal pool soils within the study region) since iron is usually bound in forms unavailable to seed plants (Wallace 1956). Belnap (1992) also showed that mucilaginous sheath material is often coated with negatively charged clay particles, providing a mechanism for retaining positively charged macronutrients in the upper soil profiles that are otherwise prone to leaching.

· Swelling *Microcoleus* mats following the retreating pool-edge waters during the "drying phase" slow evaporation, extend the wet-life of a pool, and may also produce radially-zoned rings of nutrients, inducing certain assemblages of seed plants adapted to specific requirements. A reduction in fecundity in *Limnanthes* and *Orcuttia* due to moisture stress (Brown 1976; Griggs 1976) may be moderated by *Microcoleus* crusts. Linhart (1972; 1974) provided evidence that genetic differences within populations of *Veronica peregrina* L. are adapted to specific environmental conditions differing between pool edge and basin, and may be attributed to nutrient and competition gradients. Linhart (1976) also documented that *Lasthenia* and *Downingia* have greater numbers of viable seed per head at the periphery than at the center of vernal pools. The mucilaginous mat filaments may also act as a seed trap incorporating minute seeds between the polysaccharide sheath material. Lin (1970) noted that certain *Limnanthes* species are restricted to well-defined, smaller vernal pools with conspicuous radial zonation. Seed size, micromorphology, and ornamentation in semi-aquatic plants illustrate the role of safe-site selection (possibly zonation and micro-site establishment) and colonizing ability dependent upon nutrient enriched zonal areas. Thus seed trapping in crusts, and the resulting nitrogen sink, represents an important sequestering of resources which could otherwise be lost in upland areas.

The black mats/crusts of *Microcoleus vaginatus* may also stimulate vascular plant growth and nutrient uptake by producing warmer soil temperatures during the growing season especially at higher elevations or in cooler coastal fog zones. Dark-crusted surfaces have been demonstrated to be significantly warmer than light-colored, non-crusted ones (Belnap 1995). Surface temperatures may be very important, since nitrogenase activity is an extremely temperature dependent process (Rychert, *et al.* 1978). Altered soil temperatures can also effect microbial activity and affect plant germination rates and seedling growth, since timing in vernal pool plants is essential for establishment; relatively small delays in germination can reduce species fitness and seedling establishment (Bush & Van Auken 1991). Because pool temperatures tend to follow changes in air temperature differences more closely than other aquatic environments, *Microcoleus* mats could moderate mud surface temperature fluctuations between pool center and periphery during dry-down (Alexander 1976, Linhart 1976).

Consequently, disturbance of *Microcoleus* mats/crusts can affect moisture status, nutrient availability, seed trapping and germination, seedling establishment, and competitive community structure allied to microzones developed during the recurrent flux of perimeter pool waters. This, in turn, could profoundly affect small annual seed plants in highly competitive vernal pool zones. Since vernal pool annuals produce seeds that germinate in standing water or saturated soils, and most exotic taxa do not, moisture maintenance by specialized crusts is an important resource in excluding exotic plant invasion at the pool ecotone between inundated and non-inundated habitats. Alteration of pool hydrology via reduced precipitation infiltration due to loss of cryptogamic crusts inhabiting open ground characteristic of native grasslands, may also negatively affect subsurface flows and dry-down timing in vernal pools by

decreasing water storage capacities in certain landscape types, especially in shallow soils. Subsurface flows generated by the surrounding watershed which recharge pools by lateral movement of water are important in southern California (Hanes, *et al.* 1990; Zedler 1987). Decreased infiltration rates and subsurface flows could negatively alter pool hydrology following the initial pool filling by rainfall. Pools located in native grasslands, *i.e.*, the Santa Rosa Plateau, which support diverse cryptogamic vegetation characteristic of the habitat (Riefner, unpublished data), may have increased water infiltration compared with bare or disced ground. This could significantly influence the recurrent flux of pool waters over the course of the season and contribute to pool diversity/productivity in the more arid southern portions of the state. Soil water retention capacity in combination with other biotic, geologic, edaphic, and climatic factors may significantly influence the amount and timing of subsurface flows which are important in supplementing direct precipitation and offsetting evaporative loss from pools (Hanes, *et al.* 1990).

According to terminology presented by Westman (1987), *Microcoleus vaginatus* would be identified as a "keystone species" (*i.e.*, the addition or the removal of this species could result in marked changes in community structure and function). Paine (1980) proposed that "modules" may exist within a community. Species dependent upon a common suite of resources, which disappear with the removal of a strongly interacting species, or appear with its addition, belong to a module (Paine 1980). Although there have been few detailed studies describing cryptogams as keystone species for vascular plants, a classic example is the moss *Sphagnum*, which controls the vegetation of bogs at every stage of development by impeding drainage and creating an acid habitat (Crum 1976). Recent research, however, has identified the reindeer lichen, *Cladonia rangiformis* Hoffm., as an important regulator and a keystone organism of lowland heath communities in the United Kingdom (Newsham, *et al.* 1995). Quantitative and empirical evidence discussed by Riefner & Bowler (1995) and Knops, *et al.* (1991) indicate that the fruticose (bush-like or pendulous) lichens *Niebla cerucoides* Rundel & Bowler and *Ramalina menziesii* Taylor improve moisture status and nutrient availability for vascular plant species occupying coastal cliffs and oak savannas (respectively) which concur with Westman's (1983) speculations that relatively minor differences in moisture availability between habitat sites may be sufficient to select for specific species. Vascular plant species inhabiting vernal pool zones affected by *Microcoleus* possibly include *Limnanthes* and *Plagiobothrys* in outer pool margins, and *Myosurus* and *Psilocarphus brevissimus* Nutt. which often germinate in drying cyanobacterial crusts following retreating waters. *Microcoleus* mats/crusts and associated seed plants occupying a broad radial-zone between the edge of the vernally moist zone and the muddy margin of retreating pool waters could be considered a module. The *Microcoleus* module may affect disturbed pools or clay borrow pits in the way the native nitrogen-fixing lupine (*Lupinus arboreus* Sims) alters succession by nutrient enrichment of its habitat (Maron & Connors 1996).

DISCUSSION

We propose that much of the mima mound-type topography in coastal southern California is a geologically young, dynamic landscape which formed as a result of

paleo-earthquake and liquefaction events. Conservation and management of pocket gopher colonies may play a key role in perpetuating vernal pool basins and mima mound terrain in this region. The crater pools described by Norwick (1991), as well as other pools known to have filled rapidly with silt, should be examined for evidence of pocket gopher activity to support the validity and role of the biogenic maintenance hypothesis. Vernal pool obligate plant species may gradually succumb to altered hydrologic regimes due to increased siltation in uncolonized mound-depression landscapes or in terrain abandoned by gophers. Other successional stages of liquefaction-origin pools, however, provide habitat for plant communities associated with later stages of pool formation and siltation and other organisms such as fairy shrimp. Cloudy, successional silt-pools also deter growth of certain cyanobacteria, including *Microcoleus*, which require clear water (J. Belnap, pers. comm.); thereby resulting in decreased nitrogen and water storage capacities which promote further changes in the floristic composition. Intermediate stages of siltation may be evident when vernal pool obligates appear only during abnormally high rainfall years which temporarily restore the inundation regime necessary for germination. Orcutt (1887) described a similar phenomenon in San Diego which occurred only in the unusually wet spring of 1884 when previously dry hollows and flats produced a luxuriant array of vernal pool species which "withered away to let others succeed when another favorable season should chance to roll around in future years." Earthquake successional sequences and seismogenic tracker species, that may include pocket gophers and fairy shrimp, potentially illustrate complex issues of population coevolution which remains a relatively unexplored topic in vernal pool science. The occurrence of certain locally abundant bulb-forming plants, including species of *Brodiaea* and *Muilla*, near vernal pools is often attributed to substrate preference, but may be in part due to gophers eating and storing plant parts. Previously, Brandegee (1890) discussed the "rooting of hogs" as a possible means of dispersal of *Dodecatheon* species locally distributed about vernal pools in Sacramento County.

Although the productivity of cyanobacterial mats has been described for other habitats experiencing alternate wetting-drying, *i.e.*, tidal flats (Zedler 1980), the role and potential importance of these mats in vernal pools has not been previously described. Microzone formation by *Microcoleus vaginatus* which ensures an anaerobic environment for itself and the ability to fix atmospheric nitrogen brings about a dynamic interplay between moisture storage, nitrogenase and ammonia production, and soil temperature patterns which promote rapid growth and reproduction of annual seed plants in vernal pools. Previously, Jokerst (1993) also speculated that microclimate changes due to alteration of plant cover, soil, water movement, and temperature patterns could conceivably affect herbaceous plant communities of vernal pools. Destruction of cyanobacterial associations may also permanently change composition and productivity in certain pool zones and negatively affect the loss of pool-edge moisture status and associated species. Pools altered by hydrologic and other related factors, *i.e.*, nutrient status, are often invaded by exotic taxa and dominated by relatively large populations of only a few native species. Analysis of vernal pools might assume that habitat quality is positively correlated with species density; this could be misleading for rare species conservation since density alone may not be positively correlated with habitat quality (Van Horne 1983).

Conservation issues involving successional seres of vernal pools are also relatively unexplored. Zedler (1987) considered it a mistake to assume that pools and non-pools are the only category of vegetation in vernal pool landscapes. If late successional or

disturbed silt-pools do support a dormant seed stock of obligate vernal pool species which only rarely germinate except under optimal hydrologic conditions, then these habitats should also be identified and protected, perhaps as a subclass of vernal pools. During drought years in southern coastal California, *Plantago elongata* Pursh may be an indicator of silted, drying liquefaction pools. Twisselmann (1967) indicated that vernal pools in Kern County typically exist for years without water and/or the appearance of vernal pool vegetation. Apparently, there is a continuum of water duration characteristics from which vernal pools in the strict sense and other ephemeral wetlands within vernal pool terrain develop (Zedler 1987). Other organisms, including fairy shrimp, also occupy the full range of intermittent pool types in vernal pool landscapes (Brown, *et al.* 1993). From a conservation perspective, the most practical approach is ecosystem identification proposed by Sawyer & Keeler-Wolf (1995) rather than the simplified vascular plant community classification. Species found in vernal pools that are more abundant outside pool habitat in surface water slope wetlands in coastal sage scrub, i.e., *Eryngium* aff. *vaseyi* J. Coulter & Rose and *Trifolium variegatum* Nutt., may indicate the importance of conserving small ephemeral wetlands or seepage habitats in liquefaction-type terrain. A mosaic of pool complexes incorporating distinct edaphic types and serial stages is suggested.

Cyanobacteria may play an important role in promoting maximum biodiversity in southern California's vernal pools. *Microcoleus* and/or pools designed to duplicate the recurrent flux hypothesis should be incorporated into habitat mitigation plans since artificially created pools frequently lack species abundance and cover comparable to natural pools of the same region (Ferren & Gevirtz 1990; Zedler, *et al.* 1993).

THE FLORA

This preliminary compendium of cryptogamic and phanerogamic flora is the result of surveys conducted between the spring of 1993 and the spring of 1996 at San Clemente and San Onofre State Beaches, and infrequent visits to other Orange County sites listed below. Most noteworthy is the varied composition associated with duripan or claypan soils, and cycles of abundance which vary from year to year. Several of the species recorded during this study appeared only during the unusually wet spring of 1993 (11-inches above-average precipitation; Orange County Environmental Management Agency 1996), possibly due to replenished inundation and germination regimes; other species absent or rare during wet years were recorded only during subsequent drier periods. Rare or regionally uncommon vascular plants of Orange or San Diego counties collected during this study include: *Alopecurus saccatus* Vasey, *Atriplex pacifica* Nelson, *Brodiaea jolonensis* Eastw., *Crassula aquatica* (L.) Schönl., *Deschampsia danthonioides* (Trin.) Benth., *Dudleya blochmaniae* (Eastw.) Moran, *Eryngium* aff. *vaseyi*, *Harpogonella palmeri* A. Gray *Hordeum intercedens* Nevski, *Microseris douglasii* (DC.) Schultz-Bip. subsp. *platycarpha* (A. Gray) Chambers, *Marsilea vestita* Hook. & Grev., *Muilla maritima* (Torrey) S. Watson, *Myosurus minimus* L., *Navarretia prostrata* A. Gray, *Pilularia americana* A. Braun, *Psilocarphus brevissimus*, *Psilocarphus tenellus* Nutt., and *Senecio aphanactis* E. Greene.

Voucher specimens have been deposited in the University of California, Irvine, Museum of Systematic Biology (IRVC) and selected duplicates have been placed in the herbarium of the Rancho Santa Ana Botanic Garden (RSA).

LEGEND

* Indicates a specialist which is generally restricted to vernal pools or an introduced taxon (!*) characteristic of the vernal pool community in coastal California according to Zedler (1987).
+ Indicates an aquatic generalist that is more common in other aquatic, marsh, or seepage habitats.
! Indicates a non-native species that may tolerate inundation/saturation.
o Indicates a native species occurring in diverse habitats that can tolerate limited periods of saturation/inundation.
^ Indicates a native or exotic species that may grow near vernal pools but does not grow in the saturation zone and cannot tolerate extended inundation.
† Indicates extreme fluctuations in the population size/vigor or the presence/absence of a species recorded during the study period which may be attributed to variation in environmental conditions.

R   Rare at the site.   I   Occasional to infrequent.   C   Common.

S B Surf Beach Unit, San Onofre State Beach, San Diego Duripan Vernal Pools; **Location:** San Diego County. San Onofre State Beach. Surf Beach Unit (San Onofre USGS 7.5′ Quadrangle, T9S, R7W, Section 24); **Soils:**   Soils are classified as Carlsbad gravelly loamy sand, which is gently sloping and characterized by an iron-silica cemented duripan (Soil Conservation Service 1973).

T   Trestles Unit, San Onofre State Beach, San Diego Claypan Vernal Pools and Swales; **Location:** San Diego County. San Onofre State Beach. Trestles Natural Preserve Unit (San Clemente USGS 7.5′ Quadrangle T9S, R7W, Section 14); **Soils:**   Visalia Series are mapped for this region; these have moderately rapid permeability and support soil inclusions such as Placentia soils which contain a sandy clay subsoil of very slow permeability (Soil Conservation Service 1973).

S C San Clemente State Beach, Orange County Liquefaction-Origin Vernal Pools; **Location:** Orange County. San Clemente State Beach (San Clemente USGS 7.5′ Quadrangle T9S, R7W, Section 10); **Soils:** Soils are classified as Myford Series, very slowly permeable, moderately alkaline, with a clay-rich subsoil (Soil Conservation Service 1978).

O   Additional Orange County Pools-**Locations:** Rancho Laguna-Laguna Beach (Laguna Beach USGS 7.5′ Quadrangle T8S, R8W, Section 31), Dana Hills (Dana Point USGS 7.5′ Quadrangle T8S, R8W, Section10/15), and San Clemente (San Clemente USGS 7.5′ Quadrangle T8S, R7W, Section 32); **Soils:** Myford sandy loam, rarely the moderately slowly permeable Botella clay loam (Soil Conservation Service 1978).

PRELIMINARY INVENTORY OF SPECIES INHABITING VERNAL POOLS AND ADJACENT UPLAND TERRAIN

CRYPTOGAMIC PLANTS

	S B	**T**	**S C**	**O**
CYANOBACTERIA:				
o *Microcoleus vaginatus* (Vauch.) Gom., filamentous cyanobacterium	C	C	I	I
+ *Nostoc* sp., heterocystous cyanobacterium	I	I	R	I
BRYOPHYTES:				
o *Asterella* sp., liverwort	-	R†	-	R
^ *Bryum argenteum* Hedw., moss	R	C	I	I
o *B. bicolor* Hedw., moss	-	R	R	R
o *B. gemmiparum* De Not., moss	-	-	-	· I
o *B. pseudotriquetrum* (Hedw.) Gaertn., Meyer & Schreb., moss	-	R	-	I
^ *Ceratodon* sp., moss	-	R	-	-
o *Ceratodon purpureus* (Hedw.) Brid., moss		-	R	I
^*Claopodium wippleanum* (Sull.) Ren. & Card., moss	-	-	I	I
o *Fossombria longiseta* Aust., liverwort	-	I	-	-
o *Funaria hygrometrica* Hedw., cord moss	R	C	R	I
o *Riccia glauca* L., liverwort	-	I†	-	R
o *R. nigrella* DC., liverwort	-	R	R	R
^ *R. trichocarpa* M.A. Howe, liverwort	-	R	-	I
+ *Scleropodium tourettei* (Brid.) L. Koch, moss	-	R†	-	-
^ *Timmiella crassinervis* (Hampe) L. Koch, moss	-	-	-	I
^ *Tortula ruralis* (Hedw.) Gaertn., Meyer & Schreb., moss	-	-	R	R
^ *Weisia controversa* Hedw., moss	-	-	-	R

LICHENS: (Terricolous species only; those not marked cyanolichen have green photobionts.)

	S B	**T**	**S C**	**O**
^ *Acarospora* cf. *schleicheri* (Ach.) A. Massal.	-	-	-	R
o *Caloplaca* sp.	-	-	I	-
^ *Catapyrenium lachneum* (Ach.) R. Sant.	R	-	-	R
^ *Cladonia* sp. (sterile), pyxie cups	-	-	-	R
^ *Cladonia furcata* (Hudson) Schrader	-	R	-	-
^ *Cladonia scabriuscula* (Delise) Nyl.	-	-	R	-
o *Collema* sp., cyanolichen	-	R	-	R
o *Collema texanum* Tuck., cyanolichen	R	-	R	R
^ *Diploschistes actinostomus* (Ach.) Zahlbr.	-	-	-	I
^ *Lecanora* cf. *argopholis* (Ach.) Ach.	-	-	-	R
^ *Leprocaulon microscopicum* (Vill.) Gams ex D. Hawksw.	-	-	I	R
^ *Leproloma* sp.	-	-	-	I

∧ *Psora decipens* (Hedw.) Hoffm.	-	R	-	R
∧ *Rinodina bolanderi* H. Magn.	-	-	-	R
∧ *Trapeliopsis* sp.	-	-	-	R

PHANEROGAMIC PLANTS

FERNS:
Marsileaceae, marsilea family

* *Marsilea vestita* Hook. & Grev. subsp. *vestita*, clover fern (RSA)	-	-	-	R
* *Pilularia americana* A. Braun, pillwort (RSA)	C†	-	-	-

MONOCOTS:
Cyperaceae, sedge family

+ *Eleocharis macrostachya* Britton, pale spike-rush	-	-	R	I

Iridaceae, iris family

o *Sisyrinchium bellum* S. Watson, blue-eyed grass	I	-	C	C

Juncaceae, rush family

+ *Juncus bufonius* L. var. *bufonius*, toad rush (RSA)	C	I†	C†	I
o *J. mexicanus* Willd., Mexican rush	-	-	-	I

Liliaceae, lily family

∧ *Bloomeria crocea* (Torrey) Cov., common golden star	-	R	C	R
o *Brodiaea jolonensis* Eastw., mesa brodiaea (RSA)	-	-	I†	R
∧ *Calochortus splendens* Benth., splendid mariposa lily	-	-	C	I
∧ *Chlorogalum parviflorum* S. Watson, soap plant	-	-	I	I
∧ *Dichelostemma capitatum* Alph. Wood, blue dicks	R	-	C	C
o *Muilla maritima* (Torrey) S. Watson, common muilla (RSA)	-	-	I	I

Poaceae, grass family

* *Alopecurus saccatus* Vasey, foxtail grass (RSA)	-	R†	-	-
!+ *Agrostis viridis* Gouan, bent grass	-	-	I	I
∧ *Avena barbata* Link, slender wild oat	C	I	C	C
! *Avena fatua* L., wild oat	I	I	I	I
!+ *Briza minor* L., little quaking grass	R†	-	-	-
∧ *Bromus diandrus* Roth, ripgut grass	I	R	I	I
! *Bromus hordeaceus* L., soft chess	C	C	C	I
∧ *Bromus madritensis* L. subsp. *rubens* (L.) Husnot, foxtail chess	C	I	C	C
!+ *Crypsis schoenoides* (L.) Lam., swamp grass	-	-	-	R
!+ *Cynodon dactylon* (L.) Pers., bermuda grass	R	-	R	-
* *Deschampsia danthonioides* (Trin.) Benth., annual hairgrass (RSA)	-	R†	-	-
o *Distichlis spicata* (L.) E. Greene, salt grass	R	-	C	I
! *Gastridium ventricosum* (Gouan) Schinz & Thell., nit grass (RSA)	-	-	I	R

!+*Hainardia cylindrica* (Will.) Greuter (RSA)	I†	-	R†	-
o *Hordeum intercedens* Nevski, barley (RSA)	C	-	R	C
^ *Hordeum murinum* L. subsp. *leporinum* (Link) Arcang., barley	I	-	C	I
^ *Lamarckia aurea* (L.) Moench, goldentop	R	-	I	I
! *Lolium multiflorum* Lam, Italian ryegrass	I	R	I	I
!+*Lolium perenne* L., perennial ryegrass	C	R	C	I
^ *Nassella lepida* (A. Hitchc.) Barkworth, foothill needle-grass	-	-	R	R
^ *N. pulchra* (A. Hitchc.) Barkworth, purple needle-grass	R	-	C	I
! *Phalaris minor* Retz., littleseed canary grass (RSA)	I	-	-	I
!* *Phalaris paradoxa* L., paradox canary grass	-	-	-	R
! *Poa annua* L., annual bluegrass	-	-	I	I
!+*Polypogon monspeliensis* (L.) Desf., rabbit-foot grass	C	I	R	R
! *Vulpia myuros* (L.) C. Gmelin var. *myuros*, rattail fescue	I	C	I	I
^ *V. myuros* var. *hirsuta* (Hackel) Asch. & Graebner, rattail fescue	C	C	C	C

DICOTS:
Amaranthaceae, amaranth family

! *Amaranthus albus* L., tumbleweed	-	I	R	R
o *A. blitoides* S. Watson, prostrate amaranth	-	-	R	R
^ *A. deflexus* L., low pigweed	-	-	R	R

Anacardiaceae, sumac family

^ *Rhus integrifolia* (Nutt.) Brewer & S. Watson, lemonadeberry	-	R	I	I

Aizoaceae, fig-marigold family

^ *Malephora crocea* (Jacq.) Schwantes, croceum iceplant	I	-	I	-
^ *Mesembryanthemum nodiflorum* L., slender-leaved iceplant	C	-	I	I

Apiaceae, celery family

* *Eryngium* aff. *vaseyi* J. Coulter & Rose, coyote-thistle (RSA)	I	-	-	-
! *Foeniculum vulgare* Miller, fennel	-	R	R	R

Asteraceae, sunflower family

o *Amblyopapus pusillus* Hook. & Arn., coast weed	C	-	I	R
o *Ambrosia psilostachya* DC., western ragweed	-	-	R	R
o *Baccharis pilularis* DC., coyote brush	R	C	R	R
+ *B. salicifolia* (Ruiz Lopez & Pavon) Pers., mule fat	-	R	-	-
^ *Centaurea melitensis* L., yellow star-thistle	I	-	-	R
! *Chamomilla suaveolens* (Pursh) Rydb., pineapple weed	C	-	R	R
^ *Chrysanthemum coronarium* L., crown daisy	I	-	-	-
o *Conyza canadensis* (L.) Cronq., horseweed	R	-	I	R

o *Conyza coulteri* A. Gray, Coulter's horseweed	-	I	-	-
!+ *Cotula coronopifolia* L., brass-buttons	C	-	-	R
+ *Euthamia occidentalis* Nutt., western goldenrod	-	I	-	-
^ *Filago californica* Nutt., fluffweed	-	I	-	R
^ *F. gallica* L., narrow-leaved filago	-	C	R	C
! *Gnaphalium luteo-album* L., weedy cudweed	I	I	R	I
* *Gnaphalium palustre* Nutt., lowland cudweed	R†	-	-	-
o *Grindelia camporum* E. Greene var. *camporum*, gumplant	-	-	C	R
^ *Hedypnois cretica* (L.) Dum.-Cours., Crete hedypnois	-	-	I	R
o *Hemizonia fasciculata* (DC.) Torrey & A. Gray, tarweed	C	-	I	I
o *Hemizonia paniculata* A. Gray, San Diego tarweed	-	C	I	R
! *Hypochaeris glabra* L., cat's ear	C	C	C	I
o *Isocoma menziesii* (Hook. & Arn.) G. Nesom var. *menziesii*, goldenbush	C	-	I	I
+ *I. menziesii* var. *vernioides* (Nutt.) G. Nesom, goldenbush (RSA)	-	R	-	R
! *Lactuca serriola* L., prickly lettuce	I	-	-	R
o *Lasthenia californica* Lindley, common goldfields	-	-	R	R
o *Layia platyglossa* (Fischer & C. Meyer) A. Gray, tidy-tips	-	-	-	R
o *Micropus californicus* Fischer & C. Meyer, slender cottonweed	-	I	R	R
o *Microseris douglasii* (DC.) Schultz-Bip. subsp. *platycarpha* (A. Gray) Chambers, small-flowered microseris (RSA)	C	-	R	-
+ *Pluchea odorata* (L.) Cass., salt marsh fleabane	-	R	-	-
* *Psilocarpus brevissimus* Nutt. var. *brevissimus*, woolly-heads (RSA)	C	C	R†	R†
* *P. tenellus* Nutt. var. *tenellus*, slender woolly-heads (RSA)	-	I†	R†	R†
o *Senecio aphanactis* E. Greene, rayless ragwort (RSA)	-	-	R†	R
! *Senecio vulgaris* L., common groundsel	C	-	C	I
! *Sonchus asper* (L.) Hill subsp. *asper*, prickly sow-thistle	I	-	R	R
! *Sonchus oleraceus* L., common sow-thistle	I	R	I	I
o *Stebbinsoseris heterocarpa* (Nutt.) Chambers, derived microseris	R	-	R	I
^ *Uropappus lindleyi* (DC.) Nutt., silver puffs	-	-	R	R
Boraginaceae, borage family				
^ *Cryptantha micromeres* (A. Gray) E. Greene, minute-flowered cryptantha (RSA)	-	R†	-	-
o *Harpagonella palmeri* A. Gray, Palmer's grappling hook	-	-	R	R
* *Plagiobothrys acanthocarpus* (Piper) I.M. Johnston, adobe popcorn flower (RSA)	C	I†	R†	I

^ *P. collinus* (Philbr.) I.M. Johnston var.
   fulvescens (I.M. Johnston) Higgins,
   rough popcorn flower | - | - | R | R
o *P. nothofulvus* (A. Gray) A. Gray,
   popcorn flower | - | - | - | R

Brassicaceae, mustard family
! *Brassica nigra* (L.) Koch, black mustard | - | - | R | I
o *Cardamine californica* (Torrey & A. Gray) E.
   Greene var. *integrifolia* (Torrey & A. Gray)
   Rollins, milkmaids | - | - | I | I
o *Lepidium nitidum* Torrey & A. Gray,
   shining peppergrass | C | - | I | I

Callitrichaceae, starwort family
* *Callitriche marginata* Torrey, wallow starwort | R† | - | - | -

Caryophyllaceae, pink family
^ *Silene gallica* L., common catchfly | R | - | I | R
! *Spergularia bocconii* (Scheele) Merino,
   sand-spurrey | R | R | I | . I
o *Spergularia macrotheca* (Hornem.) Heynh.
   var. *macrotheca*, sticky sand-spurrey (RSA) | - | - | R | R
! *Spergularia villosa* (Pers.) Cambess.,
   villous sand-spurrey | I | I | C | I

Chenopodiaceae, goosefoot family
^ *Atriplex lindleyi* DC., a saltbush (RSA) | R | - | R | -
o *A. pacifica* Nelson, south coast saltbush (RSA) | - | - | R† | -
! *A. rosea* L., tumbling oracle | - | - | R | R
! *A. semibaccata* R. Br., Australian saltbush | C | - | I | I
o *A. serenana* Nelson, bractscale (RSA) | - | - | R | -
! *Chenopodium album* L., lamb's quarters | - | - | I | R
! *C. ambrosioides* L., Mexican tea | - | I | R | -
! *Salsola tragus* L., tumbleweed | R | R | I | I

Convolvulaceae, morning glory family
o *Cressa truxillensis* Kunth, alkali weed (RSA) | - | - | C | I
! *Convolvulus arvensis* L., bind weed | R | - | R | R

Crassulaceae, stonecrop family
* *Crassula aquatica* (L.) Schönl., pygmy
   stonecrop (RSA) | C† | - | - | -
o *C. connata* (Ruiz Lopez & Pavon) A. Berger,
   pygmy-weed | C | I | I | C
^ *Dudleya blochmaniae* (Eastw.) Moran subsp.
   blochmaniae, Blochman's dudleya | - | - | I | R
^ *D. edulis* (Nutt.) Moran, ladies-fingers | - | - | I | I

Elatinaceae, waterwort family
* *Elatine brachysperma* A. Gray, waterwort (RSA) | I† | - | - | R†

Euphorbiaceae, spurge family
! *Chamaesyce maculata* (L.) Small, spotted
   spurge (RSA) | I | I | - | R

Fabaceae, pea family
o *Trifolium depauperatum* Desv. var. *amplectens*
   (Torrey & A. Gray) L.F. McDermott, pale
   sack clover (RSA) | C | I | - | R

o *T. variegatum* Nutt., white-tip clover (RSA)	-	-	R†	-
Geraniaceae, geranium family				
! *Erodium botrys* (Cav.) Bertol., broadleaf filaree (RSA)	I	-	R	R
^ *E. cicutarium* (L.) L'Hér., red-stemmed filaree	I	-	I	I
^ *E. moschatum* (L.) L'Hér., white-stemmed filaree	I	C	R	I
Lamiaceae, mint family				
! *Marrubium vulgare* L., horehound	_	_	R	I
Lythraceae, loosestrife family				
!* *Lythrum hyssopifolia* L., loosestrife	C	R	R	R
Malvaceae, mallow family				
! *Malva parviflora* L., cheeseweed	I	-	I	I
o *Malvella leprosa* (Ortega) Krapov., alkali-mallow	R	-	R	R
Molluginaceae, carpet-weed family				
!+ *Glinus lotoides* L., carpet-weed	-	I	-	-
Oxalidaceae, oxalis family				
^ *Oxalis pes-caprae* L., Bermuda buttercup	R	-	I	R
Plantaginaceae, plantain family				
o *Plantago elongata* Pursh, alkali plantain (RSA)	C	R	I	I
^ *P. erecta* E. Morris, California plantain	-	C	-	I
! *P. virginica* L., plantain (RSA)	-	-	-	R
Polemoniaceae, phlox family				
^ *Linanthus dianthiflorus* (Benth.) E. Greene, ground-pink	-	-	-	R
o *Navarretia atractyloides* (Benth.) Hook. & Arn., holly-leaved skunkweed (RSA)	-	-	-	R
* *N. prostrata* A. Gray, navarretia (RSA)	-	R†	-	-
Polygonaceae, buckwheat family				
! *Polygonum arenastrum* Boreau, common knotweed	R	R	R	R
!+ *Rumex crispus* L., curly dock	C	-	R	R
Portulacaceae, purslane family				
o *Calandrinia ciliata* (Ruiz Lopez & Pavon) DC., red maids	R	-	-	R
Primulaceae, primrose family				
!* *Anagallis arvensis* L., scarlet pimpernel	C	C	I	C
Ranunculaceae, buttercup family				
* *Myosurus minimus* L., little mousetail (RSA)	I	-	-	-
o *Ranunculus californicus* Benth., California buttercup	-	-	R	I
Rubiaceae, madder family				
o *Galium aparine* L., goose grass	C	-	I	I
Scrophulariaceae, figwort family				
o *Castilleja exserta* (A.A. Heller) Chuang & Heckard, purple owl's clover	-	-	R	C
^ *Linaria canadensis* (L.) Dum.-Cours., blue toadflax	-	-	I	I
+ *Veronica peregrina* L. subsp. *xalapensis* (Kunth) Pennell, purslane speedwell (RSA)	I†	-	-	-

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